The Beagle, Occasional Papers of the Northern Territory Museum of Arts and Sciences, 1986, 3(1): 195-211

PROPALORCHESTES NOVACULACEPHALUS GEN. ET SP.NOV., A NEW PALORCHESTID (DIPROTODONTOIDEA: MARSUPIALIA) FROM THE MIDDLE MIOCENE CAMFIELD BEDS, NORTHERN TERRITORY, AUSTRALIA

P. F. MURRAY
Northern Territory Museum Arts and Sciences,
GPO Box 4646, Darwin, NT 5794, Australia.

ABSTRACT

Propalorchestes novaculacephalus gen. et sp.nov. is a comparatively small *Ngapakaldia* Stirton-like diprotodontoid marsupial represented by an edentulous, extremely narrow, high braincase fragment with a marked postorbital constriction. Details of its cranial base, glenoid fossa morphology and auditory region indicate that it is aligned with the Palorchestinae. The overall morphology of *P. novaculacephalus* braincase morphology emphasizes the uniqueness of this evolutionary lineage of marsupials.

KEYWORDS: Medial Miocene, Ngapakaldia, *Palorchestes,* Diprotodontoidea.

INTRODUCTION

Placement of the enigmatic Palorchestidae among diprotodontoid marsupials was supported by the discovery of the mid Miocene species *Ngapakaldia tedfordi* (Stirton, 1967). Stirton, Woodburne and Plane (1967) placed *Ngapakaldia* Stirton close to the ancestry of *Palorchestes* Owen on the basis of synapomorphies in the auditory region and neurocranium. These features also closely aligned *Ngapakaldia* with the diprotodontidae confirming Woods (1958) diagnosis of diprotodontid affinity of *Palorchestes*, while simultaneously implying that palorchestids might lie close to the stem of the Diprotodontoidea. The key characteristics aligning these groups - the squamosal contribution to the floor of the middle ear, narrow mastoid strip on the occiput, large epitympanic fenestra, reduced postglenoid process and extensive squamosal lamina on the neurocranium - are features shared with the Vombatoidea and could be interpreted as symplesiomorphies of the greater superfamilial designation (Archer 1984). Notwithstanding, the palorchestids have greater affinity with the diprotodontoids than with the macropodoids, where they resided for decades (Owen 1874; Raven and Gregory 1946; Tate 1948) until Woods (1958), noting the lack of the large masseteric fossa in the dentary of *Palorchestes*, realigned them.

While *Ngapakaldia tedfordi* shares a number of features with *Palorchestes*, it is devoid of synapomorphic specializations in dental structure and in the development of retracted nasal bones indicating the presence of a tapir-like trunk (Bartholomai 1978). Unfortunately, the *Ngapakaldia*-like *Propalorchestes novaculacephalus* lacks these critical portions of anatomy, but preserves enough structure to indicate a closer affinity to *Palorchestes painei* Owen than does *N. tedfordi* and some functional attributes of the specimen imply specialization of the facial region. Its morphology also confirms Archer's (1984) suspicion that *N. tedfordi* is unlikely to have been ancestral to the palorchestids and it expresses a constellation of unique features that seem to enhance its distinction from the diprotodontids. There is a strong didelphoid character to the shape of the neurocranium of *Propalorchestes* in its extreme narrowness, marked postorbital and postsquamosal constrictions, lateral position of its ventral squamosoalisphenoid suture and well developed sagittal crest, in contrast to the low, broad, weakly-crested crania of most other mid-Miocene diprotodontids. Palorchestids have not previously been reported from the Bullock Creek local Fauna but in view of their presence in older and younger local faunas their occurrence at Bullock Creek was anticipated.

SYSTEMATICS

Family Palorchestidae Tate, 1948
Propalorchestes gen. nov.
Type species *P. novaculacephalus* sp. nov.

Diagnosis. Size of neurocranium intermediate between *Ngapakaldia tedfordi* and *Palorchestes painei*; narrower, higher than species of either genus; more constricted interorbitally and postsquamosally than *P. painei*, markedly more so than in *N. tedfordi;* sagittal crest longer, higher and more robust than in *N. tedfordi*; dorsal profile of cranium nearly straight in contrast to the convex profile of *N. tedfordi*; maximum cranial height at level of alisphenoid postoptic ala 94.5 mm; differs from *N. tedfordi* in having massive, long squamosal root at nearly a right angle to the lateral wall of braincase, similar in robustness and morphology to *P. painei*, depth of zygomatic arch 37.0 mm; zygomatic sulcus wider and deeper than either *P. painei* or *N. tedfordi*; longer squamosojugal suture, more closely paralleling the apparent plane of cranial base than in *N. tedfordi* or *P. painei*; zygoma less arched than in *P. painei*, similar to *N. tedfordi*. Temporal fossa of *Propalorchestes* considerably wider than in species of *Ngapakaldia* and *P. painei*; postglenoid process broad, with well developed sinus, more robust than in either *P. painei* or *N. tedfordi*; glenoid fossa in two distinct parts, flat and broad anteriorly, narrow, long and grooved posteriorly with conspicuous medial glenoid process developed on either side of the squamosoalisphenoid suture, similar to *P. painei* except for more lateral course of suture in *Propalorchestes*; epitympanic fenestra large but relatively smaller, than either *N. tedfordi* or *P. painei*; differs from *N. tedfordi* and *P. painei* in having an alisphenoid contribution to the floor of the middle ear. Features that align *Propalorchestes* with the palorchestids include the dorsolaterally extensive and ventrally invasive squamosal lamina, morphology of the pterygoid, alisphenoid and palatine remnants of the palate, the distinctive morphology of the glenoid fossa and zygomatic arch; large epitympanic fenestra and epitympanic sinus development and the presence of a narrow mastoid contribution to the external occipital wall. It is distinctive in having an alisphenoid tympanic wing contributing to the anteromesial third of the bulla, a well developed postglenoid process, narrower, higher cranium and deep supracondylar fossae on the occiput.

Derivation of name. pro (L) 'before' + *Palorchestes* (GK) 'old dancer', a genus of tapir-like marsupial = (latinized Greek) 'before *Palorchestes*.'

Propalorchestes novaculacephalus sp.nov.
(Figs 1-6)

Type material. HOLOTYPE - Northern Territory Museum (NTM) P8552-10, left and part of right side of neurocranium with most of the left zygomatic arch; partial endocranial fossa from which a latex endocast was prepared, also designated NTM P8552-10 (the endocast will be described in a separate contribution).

Diagnosis. (Compare with *Ngapakaldia tedfordi* and *N. bonythoni* Stirton) length of neurocranium from the anterodorsal lacrimal suture to the squamosal wall of the occiput 152.3 mm; maximum cranial height 94.5 mm, height of occiput from condylar remnant to supraoccipital 69.3 mm; estimated bizygomatic width 166.4 mm; interorbital width 28.0 mm; temporal fossa width 55.0 mm; shape of occiput triangular with height to width proportion of 1:1.5; narrow, deep cranial base, large pterygoid fossae, broad condylar sulcus; deeply scarred, rugose occiput for attachment of nuchal musculature; major foramina of large dimensions; well developed infratemporal crest consisting of irregular-shaped bony protuberances; stout, long posterolaterally directed postoptic ala of alisphenoid defining posterior position of narrow, possibly convergent molar alveolus; extensive endocranial sinuses resulting in inner and outer braincase walls; endocranium with minimal flexion, long, low and broad. Overall size closer to that of *N. tedfordi* than to *Palorchestes painei* but expressing substantially different dimensions in interorbital width, bizygomatic width and height to width proportions of the occiput.

Type locality and age. Camfield Beds, described by Plane and Gatehouse (1968) as "16 miles Southeast of Camfield Homestead in the north central Northern Territory." The Camfield Beds consist of light-coloured calcareous sandstone, siltstone and limestone with basal ferruginization and silicification at

Fig. 1. *Propalorchestes novaculacephalus* holotype: **A**, ventral aspect, note warping of the frontal orbital walls to the left; long, stout but low sagittal crest and punctures in the braincase, some of which closely match the shape of crocodile teeth; **B**, dorsal aspect.

the top. P8552-10 was acid extracted from a single limestone boulder collected among rubble from previous excavations in an area known informally as the 'Top Site'. The base of the cranium was encased in a band of distinctive ferruginized silicious material of which no other samples could be located in the immediate area. Age — ? middle Miocene. Fauna — Bullock Creek

Derivation of name. novacula (L) 'razor' + kephali (GK) 'head' = (latinized Greek) 'razorhead' with reference to its narrow braincase and long sagittal crest.

Description of external braincase. The braincase of P8552-10 is long and narrow, constricted in the ventral postorbital region to 28.0 mm wide relative to an estimated length of 152.3 mm from the anterodorsal lacrimal suture to the posterior surface of the mastoid (Fig. 1). Its width, estimated from the midline to the lateral surface of the squamosal immediately anterior to the glenoid fossa is 83.2 mm x 2 = 166.4 mm. A prominent sagittal crest 3.0 mm to 6.0 mm thick and 4.0 mm to 8.0 mm high extends from the occiput to the commencement of the frontal expansion. The crest is highest and thickest in the anterior third of the cranium, corresponding to the area of its greatest overall depth. The cranium is crushed, possibly slightly compressed anterolaterally and the orbital walls are warped to the left about 10°-15°. In addition to numerous cracks and crushed areas, the upper half of the cranial vault is marked by a number of large, oval punctures that match the sectional shape of crocodile teeth recovered from the Camfield Beds. In lateral view the broad, gently curving zygoma is confined to the lower half of the cranial profile (Fig. 2). The squamosal process expands dorsoventrally from a robust, rounded crest arcing inferiorly to meet the anterodorsal jugal process which includes a 16.0 mm long portion of the lateral orbital margin. The squamosojugal suture is straight and runs parallel to the apparent horizontal plane of the cranial base. The masseteric crest is

Fig. 2. *Propalorchestes novaculacephalus* holotype: **A**, lateral aspect; **B**, posterior aspect.

deepest and widest on the anterior third of the portion of jugal process present. The inferior border of the jugal is irregular and rounded on its narrow posterior margin, becoming thin and broad anteriorly. There is no evidence of a suture at the point of separation of the jugal from its missing counterpart. The width of the jugal and squamosal at 25.0 mm anterior to the jugal border of the glenoid fossa is 37.0 mm. The squamous process of the zygoma is triangular in section, measuring 30.0 mm anteroposteriorly at its base. In lateral profile, the glenoid fossa is a 23.5 mm wide notch opening obliquely posterolaterally. The length of the entire fossa, from its mesial margin half way down the medial glenoid process, to its lateral margin defined by a fine ventral crest on the jugal, is 42.0 mm. The fossa is composed of two distinct functional surfaces. The anterior surface is a shallow, oval concavity developed on a broad, low crest that becomes gradually narrower and more rounded mesially and makes a smooth, tight turn posteriorly to form the medial glenoid process. The hollowed-out, oval portion of the anterior glenoid cavity continues across the ventral squamosojugal suture and terminates in a rounded depression that occupies the entire width of the ventral surface of the jugal articulation. It is bounded anteriorly by a complexly roughened surface and a prominent torus that projects into the temporal fossa from its anteromesial edge. The ventral crest of the jugal forms its lateral boundary (Fig. 3).

The posterior glenoid concavity is a deep (3.0-4.0 mm) narrow (6.0 mm) and long (30.0 mm) groove bounded mesially by the medial glenoid process and open laterally, posterior to the preglenoid process of the jugal. Anteriorly, it is separated from the shallower articular surface by a pair of fine parallel crests that define a gently arcing, elongated transitional surface. Both articular surfaces show textural differences from the surrounding bone; the posterior groove having oblique anteroposteriorly trending striations and the anterior oval fossa having circular and oblique lines. The presence of glenoid cavity wear is a function of aging. The postglenoid process is low, broad and long. The posterior portion and crest is broken, possibly because it was fused to the missing ectotympanic. The lateral margin is 8.2 mm thick anteroposteriorly at its base and extended about 10.0 mm below the posterior glenoid surface. Its mediolateral extent is about 27.0 mm. The enormous size and clearly defined two phase functional aspect of the glenoid region is a distinctive feature of P8552-10, which will emerge in the discussion.

Propalorchestes cranial suture lines are badly obscured by fusion and by numerous cracks, depression fractures, tooth punctures and essential Bedacryl infilling for support (Fig. 4a). What can be discerned is sufficient to indicate a similarity of P8552-10 to *N. tedfordi* in having narrow, long parietals, enormously expanded squamosals and a ventrally disposed dorsal alisphenoid suture. In areal extent, the squamosal comprises about half of the braincase, extending dorsally to within 12.0 mm of the sagittal crest, 17.0 mm anterior to a line drawn vertically through the opening of the sphenorbital fissure and ventrally to comprise two-thirds of the tympanic bulla. Its vertical height from a point anterior to the glenoid fossa to the parietosquamosal suture is about 50.0 mm. Its length from the posterior squamosal crest on the occiput to its anterior parietosquamosal suture is 84.0 mm. The squamosoalisphenoid suture runs in a straight line from the medial glenoid process to the ventral infratemporal crest where it is no longer visible. Presumably it ascends the cranial wall in an arc, making a narrow contact with the long, narrow parietal wing thus separating the squamosal from the frontal. The parietal is clearly defined posteriorly, becoming lost in a depressed fracture until it reappears on the anterodorsal margin of the squamosal. The parietal is broadest at this point, but narrows into a wing where again, the sutures are lost among holes and cracks. It extends approximately 45.0 mm below the top of the sagittal crest at its inferior junction with the alisphenoid. The orbitosphenoid suture is entirely obliterated dorsally. The palatoalisphenoid suture is visible immediately inferior to foramen rotundum. Its posterodorsal contact with the orbitosphenoid is also visible but it cannot be traced anterior to the level of the ethmoidal foramen and its grooved continuation of the sphenorbital fissure. The palatine fragment retains the dorsal half of the sphenopalatine foramen, measuring 6.5 mm x 3.9 mm. The sphenopalatine foramen lies close to the

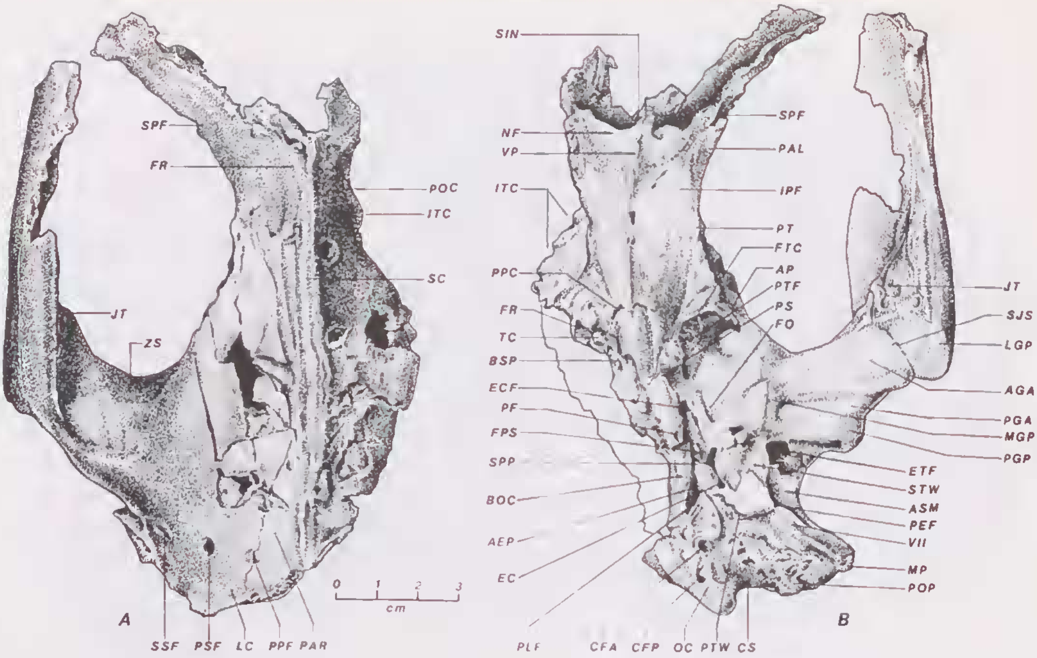

Fig. 3. *Propalorchestes novaculacephalus* holotype: **A**, structures in dorsal aspect; **B**, structures in lateral aspect. Abbreviations: **AEP**, posterior entocarotid artery; **AGA**, anterior glenoid articulation; **AP**, alisphenoid process; **ASM**, auditory superficial meatus; **BSP**, basisphenoid; **BOC**, basioccipital; **CFA**, anterior condylar foramen; **CEP**, posterior condylar foramen; **CS**, condylar sulcus; **EC**, eustacian canal; **ECF**, (anterior) entocarotid foramen, **ETF**, epitympanic fenestra; **FO**, foramen ovale; **FPS**, Foramen pseudovale **FR**, foramen; rotundum; **FTC**, foramen of transverse canal; **IPF**, interpterygoid fossa; **ITC**, infratemporal crest; **JT**, jugal tuberosity; **LGP**, lateral glenoid process; **LC**, lambdoid crest; MGP, medial genoid process; MP, mastoid process; **NF**, narial fossa; **OC**, occipital condyle base; **PAL**, palatine bone; **PAR**, parietal bone; **PEF**; posterior epitympanic fossa; **PF**; pterygopalatine foramen; **PGA**, posterior glenoid articulation; **PGP**, postglenoid process; **PLF**, posterior lacerate foramen; **POC**, postorbital constriction; **POP**, paroccipital process; **PPC**, pterygopalatine canal; **PPF**, posterior parietal foramen; **PT**, pterygoid bone; **PTF**, pterygoid fossa; **PTW**, petrous periotic tympanic wing; **PSF**, postsquamosal foramen; **SC**, sagittal crest; **SIN**, septum internal nares; **SJS**, squamosojugal suture; **SPF**, sphenopalatine foramen; **SPP**, superior periotic process; **SSF**, subsquamosal foramen; **VII**, groove for facial nerve; **VP**, vomerine process; **ZS**, zygomatic sulcus.

sphenorbital opening (40.0 mm anteriorly) the latter extending anteriorly as a 30.0 mm long, 8.0 mm deep, complex groove, 8.0 to 10.0 mm wide. Foramen rotundum is immediately posterolateral to the confluent anterior lacerate and optic foramina. The opening of the sphenorbital fissure is large, (10.0 x 6.0 mm). Foramen rotundum is approximately half the size of the former (5.5 x 4.0 mm).

The alisphenoid is produced into a stout (16.0 mm long) ventrolaterally flared pillar behind the sphenorbital and rotundum foramina which separates them from a deep, oval pterygoid fossa 17.5 x 11.0 mm in size. In contrast to most living diprotodontans, there is no abrupt transition to a horizontal shelf that defines the ventrolateral extension of the pterygoid and palatine bones for the alveolus of the molar row. The remnant palatine and alisphenoid processes of P8552-10 develop a smooth ventrolaterally curving surface, confluent anteriorly with the mesial orbital wall. The development of a long, stout ventrally disposed postoptic alisphenoid process is characteristic of diprotodontans, as it relates structually to the posteromesial position of the molar row. This structural configuration is absent in Australian marsupicarnivora, with the exception of peramelids which have an incipient development of it. In P8552-10 specific features of its configuration can be seen in *Ngapakaldia* and *Palorchestes painei*, in the exaggerated lateral flare of the alisphenoid process and pterygoids and the smooth, concave transition to the palatine alveolus, in contrast to the development of a prominent shelf-like suborbital process, clearly inscribed with a groove for the infraorbital nerve as found in phalangeroids, macropodids and diprotodontids.

The lacrimal-frontal contact cannot be discerned, although a possible lacrimopalatine suture extends inwards a few millimetres from the broken edge of the orbital wall. Dorsally, the frontal bone is entirely missing from the area normally occupied by the frontal depression. A low, oval boss near the superior margin of the break probably represents the supraorbital eminence. Warping and distortion makes some difficulty of the correct interpretation of the anteriormost extension of the sagittal crest and the commencement of its bifurcation into temporal lines. I suspect that the anterior portion is laterally compressed somewhat and that the temporal crests have been adpressed and warped to the left side of the cranium. The extreme narrowness at the postorbital contriction however, is unaffected as indicated by the absence of distortion in the thin horizontal septum that forms the roof of the inner braincase.

The back of the braincase is relatively narrow and subtriangular (Figs. 2b, 4c). The

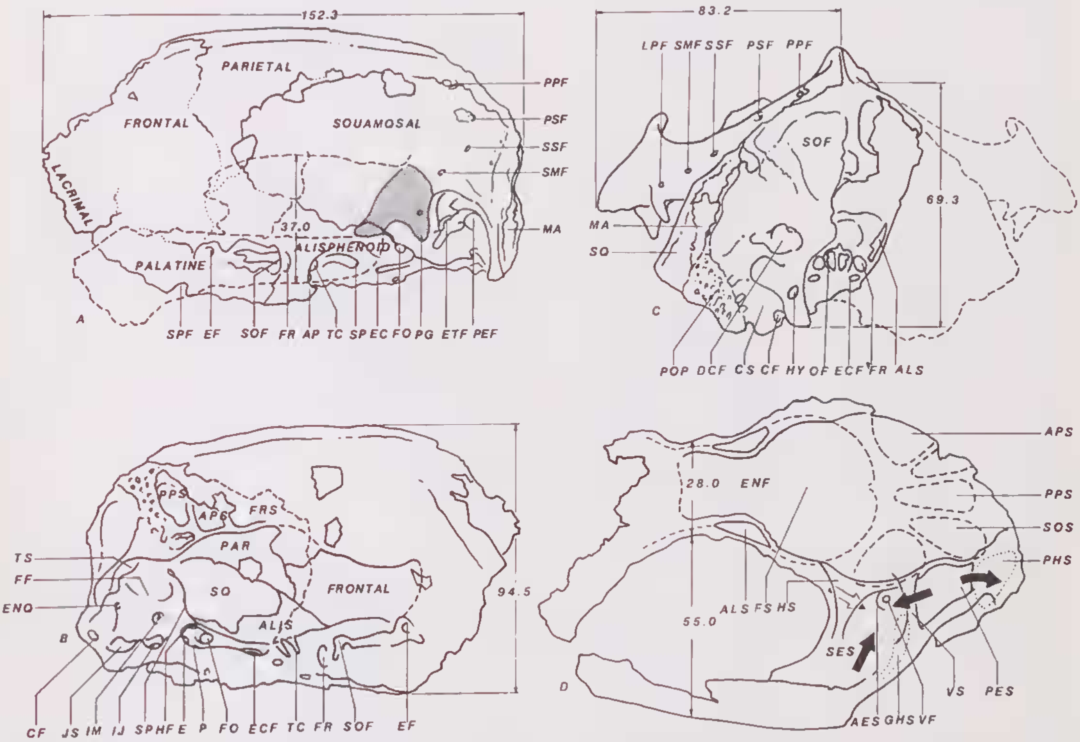

Fig. 4. *Propalorchestes novaculacephalus* holotype, lateral aspect, showing probable sutural contacts of bones of the cranial vault: **A**, solid lines represent reasonably clear sutures, stipple indicates possible sutures; **B**, endocranial sutures, frontoparietal suture is posterior to the missing area; **C**, Posterior aspect showing the narrow strip of mastoid bone interposed between the squamosal laterally and the basioccipital mesially; **D**, Auditory and non-auditory sinuses shown in dorsal aspect. Epitympanic sinuses are depicted as solid lines; dotted lines are non-auditory sinuses surrounding the inner brain case. Abbreviations: **AES**, anterior epitympanic sinus; **ALS**, anterolateral sinus; **AP**, alisphenoid process; **APS**, anterior parietal sinus; **CF**, condylar foramen; **CS**, condylar sulcus; **DCF**, doral condylar fossa; **E**, entocarotid (posterior); **EC**, **ECF**, entocarotid foramen; **EF**, ethmoid foramen; **END**, endolymphatic canal; **ENF**, endocranial fossa; **ETF**, epitympanic fenestra; *FF*, floccular fossa; **FO**, foramen ovale; **FS**, **FRS**, frontal sinus; **FR**, frontal bone; **GHS**, glenoid hypotympanic sinus; **HF**, facial nerve hiatus; **HS**, horizontal septum (squamosal); **HY**, hypoglossal or condylar foramen; **IJ**, internal jugular foramen; **IM**, internal auditory meatus; **JS**, jugular sinus; **LPF**, lateral postglenoid foramen; **MA**, mastoid; **OF**, optic foramen; **PEF**, posterior epitympanic fossa (squamosal); **PES**, posterior epitympanic sinus; **PG**, postglenoid process; **PHS**, posterior hypotympanic sinus (mastoid-squamosal); **POP**, paroccipital process; **PPF**, posterior parietal foramen; **PPS**, posterior parietal sinus; **PS**, pseudovale foramen; **PSF**, postsquamosal foramen; **RF**, foramen rotundum; **SES**, squamosal epitympanic sinus; **SMF**, suprameatal foramen; **SP**, sulcus in pterygoid fossa; **SPF**, sphenopalatine foramen; **SOF**, suboccipital fossa; **SOS**, supraoccipital sinus; **TC**, foramen transverse canal; **TS**, transverse sinus; **VF**, venous foramen; **VS**, vertical septum.

supraoccipital and/or postparietal apex is damaged. A low lambdoidal crest extends from the inferolateral squamosal to the sagittal crest where it undoubedly formed a prominent overhang in the midline. Situated a few millimetres anterior to the lamdoidal crest is a row of small, equidistantly spaced emissary foramina (sub-squamosal, postzygomatic ff., etc.) that connect with the intracranial venous sinuses. The outline of the 'occiput' is higher and narrower than that of *Ngapakaldia*, but shares with it and *Palorchestes painei*, a narrow mastoid interposition between the squamosal and the exoccipital. Immediately dorsal to the occipital condyle is a large, deep (9.0 mm) conical pit, containing on its medial aspect, an emissary foramen. Ventral to it is a deep, wide condylar sulcus encompassing a pair of condylar foramina on its medial border. The distal portion of the mastoid is broken but sufficiently preserved to indicate a wing-like transverse projection as in *Palorchestes painei*. The missing paroccipital process has a broad triangular base. Above the foramen magnum is a deep fossa for the *rectus capitus dorsalis* muscle bordered inferolaterally by a conspicuous crest that forms the mesial side of an elongated, deep, irregular crescent-shaped muscle scar that occupies the area invaded by the mastoid interpositus. The sutures are wandering and irregular in relation to its rugose surface.

Description of endocranial fossa.

Non-Auditory Sinuses: The dorsolateral relations of the thin walled inner braincase consist of a series of large sinuses and their septa (Fig. 4d). Anterodorsally, commencing from paired concave septa developed just posterior to the area of the internal coronal suture, a large frontal sinus extends anterior to the cribiform plate. The frontal sinus appears to be continuous with the narial fossa, but may have had partial transverse and vertical septa with vacuolated bony infilling. The sinus is approximately 35.0 mm high dorsoventrally and continues laterally into the alisphenoid and squamosal on the ventrolateral side. The septa separating the frontal sinus from the much smaller paired parietal sinuses form a robust bulkhead-like supporting wall over the widest part of the inner braincase. The parietal sinuses appear to have been continuous and form an arcing tunnel over the dorsoposterior part of the inner braincase. The smaller pair of lozenge-shaped parietal sinuses are located dorsal to the cerebellar chamber. These sinuses trend obliquely posteroventrally into the squamosal region and may represent dorsal continuation of the epitympanic sinuses. Grooves and small foramina perforate the floor and septa of the sinuses. These transmit small emissary vessels that conduct venous blood to larger channels emerging in the row of foramina that perforate the outer cranial wall (post squamosal, post zygomatic ff). The anterodorsal wall of the inner braincase is very thin (1.0-1.5 mm.) where it ascends over the frontoparietal lobes of the brain. Anterolaterally, the roof of the inner braincase makes contact with the outer wall forming a transverse roof of bone over the olfactory-prefrontal region that continues anteriorly to the cribiform plate. A pair of lateral sinuses are developed between the outer wall of the orbitosphenoid-alisphenoid and frontal contributions to the orbit and the olfactory tubercle and bulbar region of the inner braincase. Approximately one third of the neurocranium surrounding the endocranium is therefore hollow or partially filled with thin inflated bony processes. Extensive sinus development is present in the much larger zygomaturine and diprotodontine diprotodontoids.

In Bullock Creek *Neohelos* Stirton and related forms, the frontal and parietal sinuses are divided into cells that curve around the braincase. The interparietals and supraoccipital are similarly inflated so that the back of the brain case is essentially double walled. Among dasyuroids only *Thylacinus* Temminck and *Sarcophilus* Cuvier show an extensive anterolateral invasion of the anterior epitympanic sinus, though this double-walled condition is present in the form of shallower invaginations in all of the larger dasyurids. The development of an extensive sinus system in the larger marsupials is directly related to negative allometry of the brain. With increased body size, a greater area for the attachment of the muscles of mastication is required. In most diprotodontids the width of the braincase is greatly increased over the actual width of its proportionally small brain. In P8552-10, the increase is principally in the height of the external braincase to serve as attachment area for large temporalis muscles and is possibly related to a specialized rostrum. Its didelphoid-like shape may therefore be a secondary attribute relating to temporalis muscle emphasis. More parsimonious is a condition in which the temporalis function has been retained in *Propalorchestes*; representing a functional transistion in retaining approximately equal masseter and temporalis contributions.

Endocranial sutures: The endocranial sutures are difficult to follow throughout their course, becoming lost in a maze of cracks in the critical area of juncture dorsolateral to the middle cranial fossa (Fig. 4b). Because of the wide separation between the double walls of the braincase, the relationships of the inner and outer representations of the neurocranial lamina are difficult to interpret. However, the septa of the sinuses that connect the walls of the inner and outer braincase could provide an indication of their origin. By this criterion, the internal representation of the squamosal is sufficiently large to make contact with the frontal as in peramelids and thylacinids. The extreme alternative is that the squamosal makes no contribution at all to the inner wall of the endocranial fossa in which case there is a broad parietofrontal contact, and only a small triangular area where the squamosal keys into posterior alisphenoid and parietal sutures.

I discern that while the squamosal is indeed represented and is reasonably large, it is interposed from the frontal by a narrow anteroinferior projection of the parietal. The internal suture pattern of P8552-10 is interpreted in the following manner: the alisphenoid suture runs obliquely posterolaterally for 15.0 mm then due posteriorly for 6.0 mm. It then descends obliquely inferiorly across the temporal fossa to the superior petrosal ridge where it disappears behind the petrous periotic bone. Dorsally, the squamosal forms the posterior half of the temporal fossa, its anterodorsal extent bounded by a suture about 25.0 mm long trending across the top of the temporal fossa where it continues to ascend dorsally, immediately superior to the petrous periotic and into the superior cerebellar fossa. The coronal suture defines the anterior margin of the parietal which descends towards the alisphenoid intercranial wing in the form of a gently curved, narrow triangular process of the parietal.

The endocranial suture pattern of P8552-10 is very similar to that of *Didelphis virginiana* Linnaeus lacking a palorchestid for comparison, except that the coronal suture is situated more posteriorly, relative to the length of the braincase, indicating a greater contribution to the walls of the endocranial fossa by the frontal. The parietoalisphenoid contact is also much narrower than that of *Didelphis* Linnaeus. P8552-10 differs from the perameloid condition only in that a narrow spur of parietal interposes the anterior edge of the squamosal at the suture junctions. It is therefore structurally intermediate between the two.

Structures within the cranial fossa: The cerebellar fossa contains a pair of dorsal concavities at the midline for the vermis posteriorly and the confluence of the sagittal and transverse sinuses anteriorly. A deeply invaginated, narrow, lateral fossa accomodates the left transverse sinus and posterior portion of the cerebellar hemispheres. The thin dorsal lamina of the petrous periotic is partially missing but the entire structure is triangular in shape. The internal auditory meatus is small compared to the floccular fossa — a size related feature. It has a notch and foramen situated posterior to the internal auditory meatus for the orifice of the endolymphatic duct. Inferoposteriorly, a larger notch represents the internal orifice of the posterior lacerate foramen which continues inferolaterally into a short, longitudinally divided sinuous canal confluent with the internal opening of the internal jugular canal, for which a shallow anteroinferior notch is provided in the petrous periotic. The anterior edge of the petrous periotic apparently followed the course of the superior petrosal ridge, overlying on its squared-off, anteroinferior margin, the canal for the hiatus in the facial nerve. The concavity in the petrous bone, apparently related to this structure, is poorly developed and the margin is thick. Inferiorly there is a remnant of a long, spurlike process. The superior petrosal ridge is very prominent and sharp in P8552-10 in relation to the deep trough for foramen ovale posteriorly and foramen rotundum anteriorly. The internal fossa for foramen ovale is a large, deep tear-shaped structure 10.5 mm wide, but the actual nerve orifice is perfectly round, 5.0 mm wide and directed inferolaterally towards the mandibular foramen and muscles of mastication. In the posterior extremity of the foramen ovale fossa, a small foramen pierces the floor immediately anterior to the petrous periotic. Inferior to foramen ovale, a pair of small foramina, separated from foramen ovale by a thin lamination of alisphenoid, open posteriorly into foramen pseudovale and inferoanteriorly into the roof of the canal for the internal carotid artery. Anterior to foramen ovale, a deep, wide trough about 20.0 mm long narrows to a round, anteriorly directed internal canal for foramen rotundum. The foramen rotundum canal is very long (17.5 mm) and practically horizontal. Medial to foramen rotundum internal orifice is the large, deep oval internal carotid foramen. This structure is approximately 8.0 mm maximum diameter. Posteriorly, the canal leads to a long, straight canal of approximately 14.0 mm length before reaching its external orifice. Anteriorly, a small foramen opens into the tranverse sinus canal in the basisphenoid. The internal opening of the sphenorbital fissure commences anterior to the foramen rotundum canal. It is a widely confluent, triangular structure occupying the midline. A separate, partially enclosed canal for the ophthalmic nerve lies dorsolateral to the much larger optic-ophthalmic neurovascular

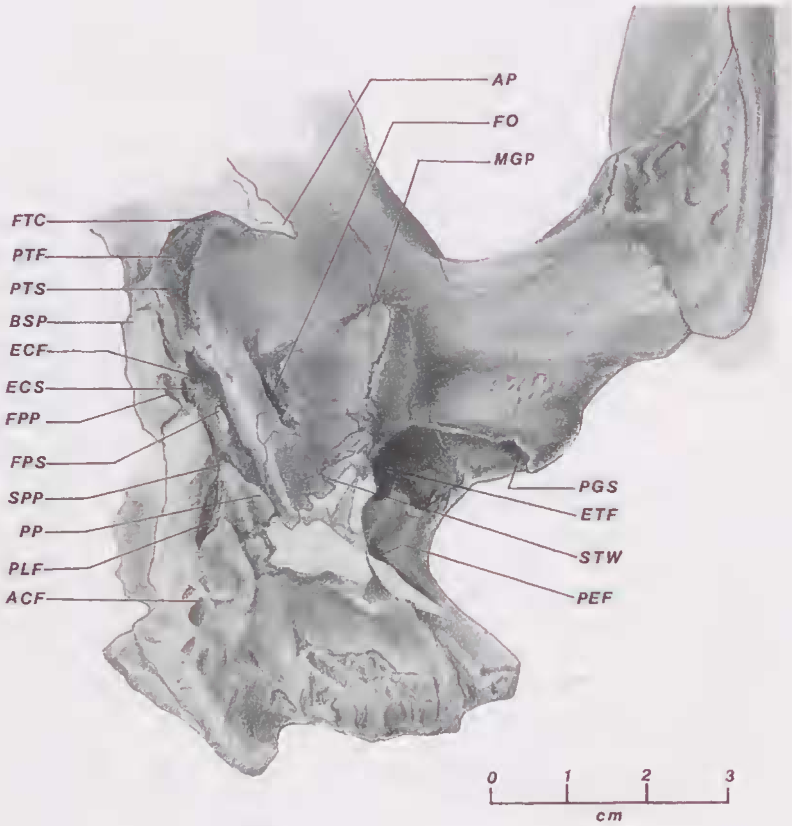

Fig. 5. *Propalorchestes novaculacephalus* holotype, ventral aspect of the auditory region. Abbreviations: **ACF**, anterior condylar foramen; **AEP**, posterior entorcarotid artery; **AP**, alisphenoid process; **ECT**, ectotympanic (remnants); **ECS**, entocarotid (anterior) sulcus and foramen; **ETF**, epitympanic fenestra; **FO**, foramen ovale; **FPS**, foramen pseudovale; **FR**, fenestra rotundum; **FTC**, foramen transverse canal; **LPF**, lateral postglenoid foramen; **MGP**, medial glenoid process; **OF**, fenestra ovalis; **PF**, **P**, pterygopalatine foramen; **PEF**, posterior epitympanic fossa (squamosal); **PF**, pterygoid fossa; **PGS**, postglenoid (glenoid hypotympostsquamosal foramen; **PTF**, pterygoid fossa; **PTS**, pterygoid sulcus; **SAS**, squamosoalisphenoid suture; **SC**, sagittal crest; **SMF**, suprameatal foramen; **SPP**, superior periotic process; **STW**, squamosal tympanic wing; **TC**, tympanic cavity; **TTY**, tegmen tympani; **VII**, groove facial nerve.

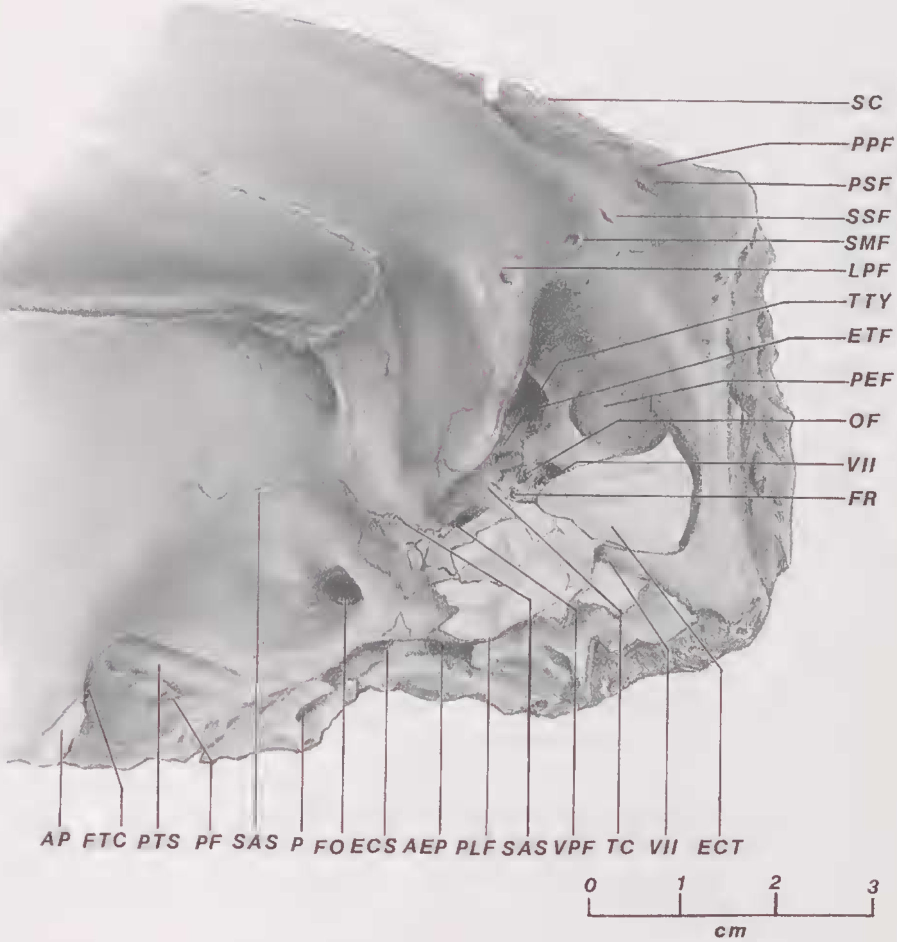

Fig. 6. *Propalorchestes novaculacephalus* holotype, ventrolateral aspect of the auditory region. Abbreviations: **ACF**, anterior condylar foramen; **AEP**, posterior entorcarotid artery; **AP**, alisphenoid process; **ECT**, ectotympanic (remnants); **ECS**, entocarotid (anterior) sulcus and foramen; **ETF**, epitympanic fenestra; **FO**, foramen ovale; **FPS**, foramen pseudovale; **FR**, fenestra rotundum; **FTC**, foramen transverse canal; **LPF**, lateral postglenoid foramen; **MGP**, medial glenoid process; **OF**, fenestra ovalis; **PF**, **P**, pterygopalatine foramen; **PEF**, posterior epitympanic fossa (squamosal); **PF**, pterygoid fossa; **PGS**, postglenoid (glenoid hypotympostsquamosal foramen; **PTF**, pterygoid fossa; **PTS**, pterygoid sulcus; **SAS**, squamosoalisphenoid suture; **SC**, sagittal crest; **SMF**, suprameatal foramen; **SPP**, superior periotic process; **STW**, squamosal tympanic wing; **TC**, tympanic cavity; **TTY**, tegmen tympani; **VII**, groove facial nerve.

orifice. The canal of the sphenorbital fissure is 19.5 mm long on the right side, where it can be measured accurately. The internal sphenorbital fissures and the internal carotid foramina lie in a broad, boat-shaped, 18.0 mm wide basin bounded posteriorly by a smooth crest, anteriorly by a midline septum and dorsolaterally by the walls of the trough that steepen and increase in height anteriorly. Sella turcica (pituitary fossa) is represented by a shallow depression formed between the right and left internal carotid orifices. The posterior portion of the basisphenoid has a pair of deep longitudinal canals. These seem rather too far posterior to be the transverse sinus canals. However, they could be connected with the internal jugular and therefore may be a continuation of the venous sinus system.

Description of Cranial base.

Morphology of the cranial base: P8552-10 has a narrow, deep cranial base (Figs 3b, 5, 6). Its minimum width is at the opening of the sphenorbital fissure where the cranium is a mere 9.0 mm wide. The ventral surface extending posteriorly from the presphenoid to the basioccipital describes a pair of diverging arcs, the convexities of which are most closely approximated in the middle of the basisphenoid about 15.0 mm posterior to the openings of the canals for the transverse sinus. Associated with this constriction are well developed ventral crests that are composed of the alisphenoids laterally and the pterygoids medially, through which passes the canal for the pterygopalatine nerve. The presphenoid-basisphenoid suture is entirely overlapped by the pterygoids which convege at the midline in a low crest.

Anteriorly, the vomer is represented by a thin blade-like process that separates the roof of the internal nares and may have made contact with the midline of the palate. Deep choanal fossae are developed on either side of the palatovomerine septum. The floor of the orbital region is a broad, convex surface that abruptly terminates posteriorly about 10.0 mm behind foraman rotundum in a stout pillar of bone that flares laterally towards the glenoid fossa. This structure indicates the posterior extension of a long posterior palatine process and posteriorly forms the anterior wall of a deep pterygoid fossa. Its broken ventral surface indicates that a thin lamina of pterygoid formed a floor for the fossa and probably continued posterolaterally in the form of a crest that reached the tympanic wing on its anteromedial surface, ventral to foramen ovale. It seems unlikely that the pterygoid alae flared laterally much more than what is represented on the fossil. A similar buttressing of the postoptic - postpalatine region is present among diprotodontids and macropodids where it forms the posterior margin of the alveolar shelf. As noted, *Propalorchestes* and *Palorchestes painei* are synapomorphic in the morphological detailing of this region. The pterygoid fossa contains two foramina, both of which enter the transverse canal in the basisphenoid. Posterior to the larger of the two foramina is a deep, wide sulcus of approximately the same diameter as the foramen. The sulcus ends posteriorly on a ventrally disposed crest of the alisphenoid which forms the lateral margin of the internal carotid canal and foramen medially and the floor of the large, round foramen ovale laterally. It continues to the alisphenoid portion of the tympanic wing of which it is a part, the crest forming the lateral wall of foramen pseudovale. The medial and lateral walls and floor of the internal carotid canal and margin of the foramen are damaged, the actual extent of the canal, as opposed to the foramen, being difficult to determine. It is likely that the canal lay in a sulcus confluent with foramen pseudovale and was partially roofed by a crest arising from the pterygoid and basisphenoid, continuing posteriorly as the alisphenoid. The actual orifice of the internal carotid foramen was probably an elongated oval shape. A posterior entocarotid canal cannot be readily differentiated from the large, elliptical posterior lacerate foramen that opens immediately mesial to the petrous periotic. Except for a low crest on the latter, partially dividing the foramen, there is no other indication of its presence.

The basisphenoid-basioccipital suture is located immediately posterior to the internal carotid foramen. In a bilateral restoration, a narrow trapezoidal shape of the bone is indicated, with a lateral expansion between the posterior lacerate foramen and the entocarotid foramen. Both the basisphenoid and the basioccipital surfaces extend a considerable distance inferior to these openings — that is — they are situated well within the lateral margins of the posterior basicranial axis rather than developed level with the ventral surface of the cranial base. This is a reflection of a pronounced posteroventral convexity of the basisphenoid. Paired condylar foramina (condylar and hypoglossal ff.) pierce the basioccipital a short distance posterior to the posterior lacerate and internal jugular foramina. They lie in a wide, shallow sulcus between the broken process for the occipital condyles medially and the damaged base of the paroccipital and mastoid processes laterally.

Auditory Region: A general feature of the tympanic region of P8552-10 is its mesial confinement, as though crowded towards the basisphenoid suture by the wide and invasive squamosal root with its enormous glenoid fossa and correspondingly broad postglenoid process (Figs 5, 6). The auditory region is damaged and partially obscured by siliceous matrix, although its basic morphology can be appraised. The tympanic wing of the auditory bulla is predominately derived from the

Table I. Raw comparison of character states of 38 structures of the neurocranium of *Propalorchestes novaculacephalus* (P8552-10) with various diprotodontan taxa based on a subjective rating of the expression of a morphocline from O = absent to 5 = highly developed.

	Phalangeroids	*Macropodoids*	*Vombatids*	*Thylacoleonids*	*Phascolarctids*	*Zygomaturines*	*Diprotodontines*	*Palorchestids*	*Wynyardiids*	*P8552-10*
Parietal width	5	4	2	5	3	2	1	1	3	1
Squamosal lamina	4	2	4	3	3	5	5	5	3	5
Squamosal tuberosity	4	2	4	1	3	5	5	5	3	5
Squamosal tympanic wing	0	0	3	3	5	5	4	3	3	3
Thickness tympanic bulla	2	4	3	3	4	3	4	1	—	1
Size tympanic bulla	5	1	1	1	5	2	2	2	2	2
Epitympanic fenestra	0	0	5	0	2	1	2	5	3	3
Posterior epitympanic fossa	1	1	3	2	2	1	2	4	1	4
Epitympanic sinuses	1	1	2	2	2	4	4	4	2	5
Non-auditory sinuses	0	0	1	0	0	5	5	5	0	5
Postglenoid process	4	1	0	4	5	4	2	1	3	4
Medial glenoid process	2	1	3	4	3	4	1	5	1	5
Lateral glenoid process	0	0	1	2	5	0	0	5	2	5
Complexity glenoid fossa	1	1	1	1	3	3	2	5	3	5
Postorbital constriction	2	4	3	2	2	4	1	5	5	5
Postglenoid constriction	2	4	3	2	2	4	1	5	5	5
Width neurocranium	4	2	4	4	4	3	3	3	2	1
Mastoid interpositus	0	0	5	5	0	0	3	4	—	3
Dorsal condylar fossa	0	0	2	2	2	2	2	—	—	5
Zygomatic curvature	2	3	2	4	2	3	4	5	2	3
Zygomatic width	3	4	3	4	3	3	5	5	3	5
Temporal fossa width	2	4	4	5	2	2	2	3	3	5
Sagittal crest	2	0	0	3	0	3	0	2	5	5
Lambdoid crest	2	2	2	5	2	1	1	3	4	5
Mastoid process	2	3	3	3	3	1	1	3	—	3
Paroccipital process	2	5	5	3	5	3	2	2	—	2
Everted inf. al. proc.	0	3	0	0	0	0	0	5	0	5
Infraorbital shelf	3	5	5	0	5	5	5	0	4	2
Vomerine septum	1	0	1	5	3	0	0	—	3	3
Narial fossa	0	0	1	5	2	0	2	—	3	5
Interpterygoid overlap	2	5	2	2	3	5	5	5	4	5
Pterygoid fossa	1	5	3	2	1	3	1	4	3	4
Pterygoid sulcus (c.t.s.)	0	5	3	2	1	3	1	4	3	4
Postglenoid arch	4	3	4	2	3	3	1	5	4	5
Entocarotid groove	0	0	5	0	0	5	1	3	2	3
Basisphenoid crest	0	0	5	2	3	2	1	3	1	3
Alisphenoid crest	0	0	5	0	0	3	3	4	4	5
Condylar Sulcus	0	0	2	0	0	5	3	5	—	5

squamosal. The squamosoalisphenoid suture is clearly visible as it traverses the crest of the medial glenoid process. It then becomes lost among cracks, but appears to trend obliquely posteromesially to encompass ½ to ⅔ of the bulla, depending on the original extent of the structure, as the original shape of the tympanic bulla cannot be determined due to damage. It was certainly small, subrectangular, perhaps and appears to have been incomplete or extremely thin walled posteriorly. A thin bony crest arising either from the mastoid or the petrous periotic may have formed its posterior wall. The oval epitympanic fenestra is exposed in the superficial meatus, its lateral wall interrupted by a break that exposes a deep tubular sinus within the postglenoid process. The posterolateral wall of the epitympanic fenestra measures approximately 12.0 mm x 16.5 mm. Its mesial wall is damaged. Posteromesially, a stout process of squamosal appears to have formed an arched lateral portion of the roof of the very confined tympanic cavity. It was continuous with or made contact with a horizontal process that extends posteriorly from a long, thin vertical septum that divides an enormous epitympanic sinus into an anterior and posterior portion (Fig. 4d). Its posteroinferior wall forms a wide facial sulcus, the nerve of which, although its course is interrupted by matrix and perhaps remnants of the ectotympanic, appears to pass out of the auditory region in a long, shallow groove in the anterolateral surface of the mastoid. The tympanic cavity is approximately 6.0 x 6.0 mm in diameter and extends mesially as a deep hollow dorsolateral to the scarcely visible lateral wall of the petrous bone. The small fenestra ovalis is visible in lateral view approximately 4.0 mm anteroventral to the facial foramen. Fenestra rotundum is located approximately 3.0 mm inferior to fenestra ovalis. *Propalorchestes* is therefore more like *N. tedfordi* than *Palorchestes painei* in having the sulcus facialis posterior to and on a level between the fenestrae. Also preserved is the rounded incudal fossa and a small bony spur which may represent the attachment of the suspensory ligament of the malleus. Immediately within the facial sulcus is a shallow groove that appears to have accommodated the tympanic. The tympanic and its absent membrane were therefore comparatively small structures.

The petrous periotic is exposed in a large, triangular depression bounded posteromedially by foramen lacerum posterior and the confluent posterior entocarotid canal; posteriorly by the mastoid wall; anteriorly by the long, wide entocarotid groove and its thin roof; anterolaterally by a narrow opening from above the tympanic wing that probably represents the eustacian canal. The superior periotic process makes contact with the basioccipital immediately posterior to its most lateral expansion. The promontorium is a broad, triangular dorsolateral expansion defined anterolaterally by a cleft above which fenestra rotundum is located. Fenestra rotundum is not visible in ventral aspect. Partially visible is a dorsolateral extension of the periotic that represents the tegman tympani. The ventral surface of the periotic is developed into a thick rounded crest that may contribute a wing to the posterior wall of the tympanic bulla. Dorsomedially, the petrous periotic wings over a short deep sinus, divided by a thin triangular process into a dorsal and ventral channel which is confluent posteriorly and terminates in a deep, round fossa with a foramen penetrating its roof; part of the system of channels representing the internal jugular-sigmoid and transverse sinus anastomoses. The anterodorsal portion may have accomodated an arterial branch from the posterior entocarotid. Nerves IX, X and XI must also traverse the posterior lacerate foramen, presumably along the course of the internal jugular vein.

The dorsal portion of the medial side of the internal petrous periotic is absent. There is a broad depression corresponding to the maximum depth but not the total circumference of the floccular fossa. The ventral half of the fossa is preserved indicating that it was a broad, shallow depression. The internal auditory meatus is developed with a broad, shallow, elliptical depression on the ventromedial surface of the petrous bone. A septum dividing the facial from the vestibuloacoustic nerve is located deep within the foramen. The posterior margin of the petrous is damaged in the area of the orifice of the endolymphatic duct. It appears to have a broad, shallow depression associated with it that extends anteriorly to the posterior margin of the internal meatus. The endocranial portion of the petrosal is approximately 20.5 mm long dorsoventrally and 18.5 mm wide, oriented perpendicularly and lies at an angle of approximately 6O° in the endocranial wall relative to the sagittal plane.

SUMMARY AND CONCLUSION

Propalorchestes novaculacephalus is slightly larger than *N. tedfordi* and slightly smaller than *Palorchestes painei*. The cranium is relatively narrower and higher overall than the species of either genus. The squamosal root is longer and more closely approximates a right angle in its slightly anterior and primarily lateral projection to the zygoma. Consequently, P8552-10 has a wider, narrower and deeper zygomatic sulcus than either genus. The squamosal zygoma is deeper than in these forms and the squamosojugal suture is longer than in *P. painei* and closer to paralleling the plane of the cranial base than it is in the species of either genus. The zygoma is less arched than in *P. painei*, approximating that of *N. tedfordi*. The temporal fossa of P8552-10 is much wider than in either genus. The maximum height of the cranium occurs far anterior to that of either *P. painei* or *N. tedfordi*. The dorsal profile of the cranium differs from that of species of both genera in being relatively straight rather than markedly convex at a vertical intersection with the postoptie ala of the alisphenoid. P8552-10 differs from *N. tedfordi* and *P. painei* in having a comparatively smaller epitympanic fenestra and a well-developed postglenoid process. In P8552-10 the fenestra ovalis is directly dorsal to the fenestra rotundum as in *N. tedfordi*. The facial foramen is posteriorly disposed and slightly dorsal to fenestra ovalis, thus differing from either *P. painei* or *N. tedfordi*. However, the suleus facialis is posterior to and at a level intermediate to the two fenestrae as in *N. tedfordi*. P8552-10 has an irregularly shaped mastoid strip that ascends the external mastoid wall of the lateral occiput as in diprotodontids and vombatids. It differs from *N. tedfordi* and probably *P. painei* in having deep supracondylar fossae with a large emissary foramen (supracondylar f.) in its medial wall.

P8552-10 has a foramen ovale of large diameter bridged by an oblique crest of alisphenoid and deeply excavated on its mesial surface by a wide entocarotid groove. This region is damaged in casts examined by me of *N. tedfordi* and *P. painei*. The foramen ovale is vertieally oriented and in total view from a lateral aspeet in P8552-10. A series of shallow grooves radiate from the anterodorsal surface of foramen ovale in *Propalorchestes*. These grooves appear to be present in *P. painei* indicating that a similar morphological detail was present.

The postsquamosal constriction is much more pronouneed in P8552-10 than it is in *P. painei* or *N.tedfordi*. It is doubtful that the transverse flare of the mastoid and squamosal erest of the oeciput approaehed that of *P. painei*. Notwithstanding, there is general morphologieal agreement between P8552-10 and *P. painei* in the profile and in the morphology of the ventral occiput. These points of agreement include the presenee of a deep, wide, eondylar suleus and the precipitous anterior wall of the paroceipital and mastoid process behind the petrous bone. Poe's illustration of *P. painei* suggests that the posterior border of the epitympanic fenestra and, by proximity, the floor of the middle ear is developed from a thin bony flange of the mastoid (Woodburne 1967). P8552-10 suggests this possibility. However, it seems to be more intimately related to the petrous in *Propalorchestes*. In any case, the petrosal and the posterior wall of the epitympanic fenestra are close to the anterior wall of the mastoid in both P8552-10 and *P. painei*.

The diagnosis of *Propalorchestes* as a palorchestid rests on synapomorphic features including 1) the morphology of the glenoid fossa; 2) the morphology of the alisphenoid-ptergyopalatine processes in relation to the alveolus; 3) the squamosal involvement in the tympanic bulla; and 4) the mastoid interpositus in the occiput. This strongly suggests an interrelated functional and developmental complex that is unlikely to develop as a parallelism. *Propalorchestes* is generally more primitive and simultaneously more specialized than *Palorchestes painei*. The pronounced sagittal crest, wider temporalis fossa, narrower anteroposterior dimension of the zygomatic sulcus and apparently even more robust zygomatic arches indieate that powerful masticatory forces, possibly surpassing those exerted by the larger *P. painei*, were required by this comparatively small diprotodontan. The stout alisphenoid strut behind the sphenorbital fissure and foramen rotundum, combined with its curving, slightly flared palatine remnant, are also indicative of extraordinary masticatory forces relative to the animal's size. The apparent lack of an abrupt transition laterally to form a suborbital shelf for the molar alveolus is similarly a modification for reducing bony strain to the posterior palate. These features are all present in *P. painei* to approximately the same degree of development as P8552-10 but on a larger, wider eranial base and broader neurocranium. The glenoid structure is of the same unique type in both, although in P8552-10 the postglenoid process is comparatively more robust, longer and probably wider. It is still a modest structure eompared to the postglenoid process development in, for example, a Bullock creek *Neohelos* sp. but seems to indicate a proportionally larger eondyle and heavier dentary in P8552-10 than in *P. painei*. P8552-10 differs also from *P. painei* and *N. tedfordi* in having a smaller epitympanic fenestra. This could be functionally related to the proportionally larger glenoid and longer squamosal tuberosity anteriorly and the wider postglenoid arch posteriorly, combined with the overall narrowness of the cranium, but more likely it is an expression of structural conservatism.

The occiput of P8552-10 is narrower and higher than in *P. painei* and *N. tedfordi*. The muscular attachments indicated by deep fossae and prominent crests indicate that the nuchal musculature in these palorchestids was highly developed, certainly more so than it was in *N. tedfordi*. The large fossa for the *rectus capitus posterior major* muscle indicates that a powerful elevator of the head was required, either to support a very heavy skull or to assist in elevating the head for feeding. The deep pits for tendinous insertions of the *rectus capitus posterior minor* muscles imply that powerful pulling moments were exerted on the occipitoatlantic joint. The large lateral scar probably served mainly as the insertion for the *obliquus capitus superior*, another elevator of the skull.

The construction of the cranial base and its associated foramina is essentially plesiomorphic among diprotodontans. Similarly, the endocranial fossa, its internal suture pattern and lack of internal basicranial flexion are reflections of this plesiomorphy which is similar to didelphoids and Australian polyprotodonts. It is however conceivable that the lack of brain flexion could be associated with the possible specializations of the facial skeleton. I am inclined to conclude that the entire basicranial-endocranial complex is conservative, symplesiomorphic with the stem diprotodontans and indicative of an early separation of palorchestids from diprotodontids. However it is conceivable that the relationship of *N. tedfordi* to *Palorchestes* is likely to be modified by *Propalorchestes novaculacephalus*. It is improbable that the very generalized morphology of *N. tedfordi* or *N. bonythoni* could lie in direct ancestry to *Propalorchestes* within the confines of the Medial Miocene. The generalized tooth morphology, wide cranial base and collective synapomorphies of *Ngapakaldia* with other medial Miocene diprotodontids indicate that the genus progressed further with the diprotodontids than with the more plesiomorphic palorchestids. Within the framework of our present state of knowledge, *Ngapakaldia* is an excellent candidate for a sister taxon the palorchestidae. From the same frame of reference, *Propalorchestes* might also lie in an indirect relationship to *Palorchestes* with respect to its conservative middle ear region and moderate degree of development of the epitympanic fenestra. Therefore the genus *Palorchestes* might eventually be recognized as a contemporary of both *Propalorchestes* and *Ngapakaldia*. Alternatively, some degree of parallel evolution must have been involved in the reduction of alisphenoid contribution to the middle ear, reduction of the postglenoid process and enlargement of the epitympanic fenestra in *Propalorchestes novaculacephalus* if it was directly ancestral to *Palorchestes*.

ACKNOWLEDGMENTS

My sincere thanks and gratitude are extended to Dirk Megirian, Mike Archer, Allan Howard and Lorna Watt.

REFERENCES

Archer, M. 1984 The Australian Marsupial Radiation. M. Archer and G. Clayton (eds) *Vertebrate Zoogeography and Evolution in Australasia*: 633-808. Hesperian Press: Western Australia.

Bartholomai A. 1978 The rostrum in *Palorchestes* Owen (Marsupialia: Diprotodontidae) results of the Ray E. Lemley Expeditions, part 3. *Memoirs of the Queensland Museum* **18**: 145-149.

Owen, R. 1874 On the fossil Mammals of Australia part IX family Macropodidae; Genera *Macropus, Pachysiagon, Leptosiagon, Procoptodon and Palorchestes*. 2 Volumes. *Philosophical Transactions of the Royal Society*: London.

Plane, M. and C. Gatehouse 1968 A new vertebrate fauna from the Tertiary of Northern Australia. *Australian Journal of Science* **30**: 271-273.

Raven, H. and Gregory, W. 1946 Adaptive branching of the Kangaroo family in relation to habitat. *American Museum Novitates* **1309**: 1-33.

Stirton, R. 1967 The Diprotodontidae from the Ngapakaldi fauna, South Australia. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics Australia* **85**: 1-44.

Stirton, R. Woodburne, M. and Plane, M. 1967 A phylogeny of the Tertiary Diprotodontidae and its signiface in correlation. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics Australia* **85**: 149-60.

Tate G. 1948 Results of the Archbold Expeditions, No 59. Studies on the Anatomy and Phylogeny of the Macropodidae (Marsupialia). *Bulletin of the American Museum of Natural History* **91**: 233-352.

Woodburne, M. 1967 The Alcoota Fauna, Central Australia: an integrated paleontological and geological study. *Bulletin of the Bureau of Mineral Resources, Geology and Geophysics Australia* **85**: 53-103.

Woods, J. 1958 The extinct Marsupial genus *Palorchestes* Owen. *Memoirs of the Queensland Museum* **13**: 177-193.

Accepted 19 September 1986